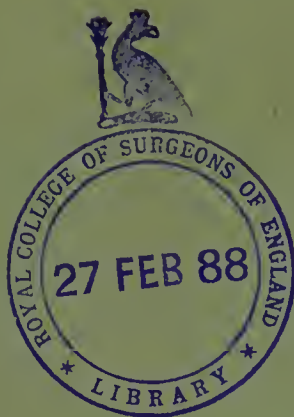


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EXPERIMENTS
ON
SPECIAL SENSE LOCALISATIONS IN
THE CORTEX CEREBRI OF THE MONKEY.

BY E. A. SCHÄFER, F.R.S.,

Jodrell Professor of Physiology in University College, London.

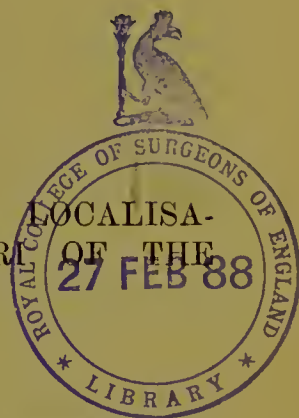


[Reprinted from 'BRAIN,' Parts XXXIX. and XL.]

EXPERIMENTS ON SPECIAL SENSE LOCALISA-
TIONS IN THE CORTEX CEREBRI OF THE
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IN the long series of experiments upon the monkey's brain with which I was engaged in conjunction with Mr. Victor Horsley during more than two years,² we obtained as the result of lesions of certain parts of the cortex indications, more or less marked and permanent, of the partial or complete abolition of certain special sense functions, while others remained to all appearance intact, no matter what portion of the cortex might be implicated in the lesion. The sensory impressions, the perception of which was thus interfered with, were those of sight and touch, and associated with loss of the latter was impairment of general sensibility. On the other hand, we did not obtain in any of our experiments unmistakable evidence, nor indeed any evidence at all, of the impairment or abolition of the senses of hearing, smell, or taste.

With regard to vision, our experiments were not conclusive. We found that extensive lesions, both of the occipital lobe and of the temporal lobe, were invariably followed by visual disturbances, taking the form, when the operation was confined to one side of the brain, of bilateral homonymous hemianopsia; but in nearly every case the hemianopsia was merely temporary, and after a certain time we could not in

¹ The experiments to which this article relates have, for the most part, been performed in conjunction with Dr. Sanger Brown, of New York. The details of our observations, with representations showing the exact post-mortem condition of the brains operated on, are given in a paper submitted by us to the Royal Society, which was read at the meeting of that Society on December 16th, 1887.

² Horsley and Schäfer, "A Record of Experiments upon the Functions of the Cerebral Cortex," 'Philosophical Transactions,' 1888.

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our monkeys obtain any distinct evidence of the persistence of the visual defect. The most marked results of this kind were obtained when the occipital lobes were the seat of the operation, extensive unilateral lesions in this region producing hemiopia, and bilateral lesions producing amblyopia; but in neither case were the symptoms permanent, and after a time the animals, so far as we were able to determine, could see as well as their intact fellows. In one case only did the hemiopia persist, and this was one in which, after a bilateral lesion of both occipital lobes had been carried out and the temporary blindness thereby produced had been recovered from, the angular gyrus of one side was destroyed. This second operation, made upon an animal in which the occipitals had already been extensively destroyed *without* permanent blindness, did produce a condition of hemianopsia which lasted until the animal's death some three months later. We were of opinion, at the time, that this instance might warrant us in taking up a position similar to that of Luciani and Tamburini,¹ and intermediate between those of Ferrier and Munk—the former of whom originally denied the participation of the occipital lobe in the visual perceptive function, and still appears to regard it as subordinate to the angular gyrus; whereas the latter would localise those perceptions entirely in the occipital lobe, and deny all participation of the angular gyrus. But we made only four experiments upon these regions, and in none of them was the removal of the occipital lobe complete, as was proved by post-mortem examination of the brains. They were not, therefore, decisive against Munk's statement, that persistent hemiopia or blindness follows extirpation of one or both occipital lobes alone, and it became necessary to pursue further enquiries in order to test its accuracy.

This I have now accordingly done, in conjunction with Dr. Sanger Brown. With reference to visual perceptions, we have experimented both upon the angular gyri and upon the occipital lobes.

In one monkey, a small, active and intelligent *Rhœsus*, we

¹ Luciani and Tamburini, "Sulle funzioni del cervello; seconda comunicazione," 'Centri psico-sensori corticali,' 1879. (Abstract in 'BRAIN,' Vol. II.)

destroyed, as completely as we could from the surface by the actual cautery, the grey matter of one angular gyrus. We tested the sight immediately after complete recovery from the anæsthetic, but could discover no defect of vision, nor any loss of movement of the eyes or eyelids, nor any anæsthesia of the cornea or conjunctiva. When the eye of the same side was closed by plaster, the animal continued to see perfectly well with the eye of the other side, nor could we discover any diminution in the visual field.

The same tests were applied, from time to time, during the few days succeeding the operation; and as completely negative results were invariably obtained, we proceeded to destroy in the same manner, a week after the first operation, the angular gyrus of the opposite side. This lesion also was not followed, either immediately or at any subsequent time, by any visual defect that we could discover by the most careful tests we knew how to apply. That the lesion was complete on both sides was proved by the post-mortem examination, which was made some months later (see Fig. 1). Here, then, was a

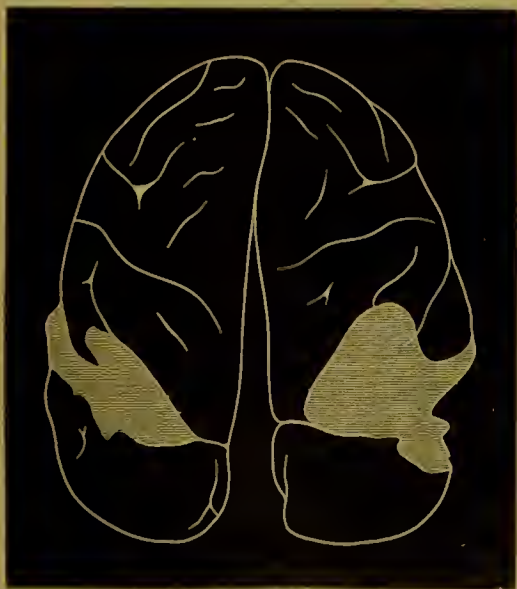


FIG. 1.—Brain of a Monkey, with complete destruction of both angular gyri. Viewed from above.

monkey with total absence of the cortex of both angular gyri, without exhibiting at any time any appreciable defect either in

its visual perceptions or its ocular movements, or in the sensibility of the globe of the eye. This animal was kept for several months, was examined carefully not only by ourselves but by many other people, and was exhibited to the Neurological Society at its meeting in this laboratory last winter.

A single well-marked negative case like this is conclusive against the idea, that in the monkey cerebral visual perceptions are *localised* in the angular gyri. As already stated, this idea was formerly entertained by Dr. Ferrier;¹ but it rested, apart from general analogies, chiefly upon experiments which were at that time, before the days of antiseptic surgery, necessarily somewhat rough. In consequence of his more recent experiments, undertaken in conjunction with Professor Gerald Yeo,² Dr. Ferrier has somewhat modified his earlier conclusions. In the 'General Results' of their experiments on the occipito-angular region (*op. cit.* p. 504) we find the following statement:—

"Complete destruction of the angular gyri on both sides causes for a time³ total blindness, succeeded by lasting⁴ visual impairment in both eyes. Destruction of the convex aspect of the angular gyrus on one side causes temporary abolition or impairment of vision in the opposite eye. The defect is not of a hemiopic character. Subsequent similar lesion of the other angular gyrus causes bilateral visual defect, also only of transient duration."

And elsewhere⁵ Dr. Ferrier gives it as his mature opinion, that "the angular gyrus is the special region of clear or central vision of the opposite eye, and perhaps to some extent also of the eye on the same side."

These statements and opinions are not consonant with our results in the case of the monkey we have above described. Even half an hour after the operation on either side we obtained no evidence whatever of defective vision, the animal being at the time quite lively and having recovered from the

¹ See the first edition of his book on the 'Functions of the Brain.'

² Ferrier and Yeo, "On the effects of the lesion of different regions of the Cerebral Hemispheres," 'Philosophical Transactions,' 1884.

³ Three days, *op. cit.* pp. 493, 494.

⁴ Observed, however, for one month only, p. 494.

⁵ 'Functions of the Brain,' 2nd edition, 1886, p. 288.

chloroform. It is true we did not simultaneously remove both angular gyri, and could not therefore, according to Dr. Ferrier's results, expect to get total blindness even immediately after the destruction of the second gyrus. But we should in each case have obtained temporary blindness of the opposite eye (not hemiopia), whereas we got no appreciable result whatever. Since, however, it might be objected, that although we destroyed the cortex of the angular gyrus right up to the fissures bounding the gyrus, we had still left that at the bottom of these fissures, we determined in another animal to make a complete removal of the gyrus angularis in its whole depth and extent. We accordingly separated the lips of the fissures, and scooped away the entire gyrus angularis of one side, producing thereby a gap in the surface of the brain of considerable depth. This operation *was* followed by a disturbance of visual perceptions; but the disturbance was not amblyopia; it was distinctly hemiopic. The condition lasted for a few days, gradually passing off, leaving vision unimpaired. The result, although somewhat different from that which we obtained from the destruction by cauterisation of the exposed grey matter, by no means corresponds to Dr. Ferrier's results, nor does it fit in with his conclusions; and, as will presently appear from our experiments upon the occipital lobe, it is susceptible of an interpretation which would exclude the angular gyrus from participation in the function of cerebral visual perception, for the result can be explained by the vascular disturbance which is produced in that lobe by so radical a removal of the neighbouring gyrus.

We may remark incidentally, that neither this case nor the other one with (successive) double extirpation of the gyrus angularis offers any support to the statement of Professor H. Munk, that the convolution in question is related to the sensibility of the opposite eyeball and concerned in regulating its movements.¹ On this point we entirely agree with Dr. Ferrier, who states that he has "never seen, either on unilateral or bilateral destruction, the slightest appearance of ptosis or paralysis of the ocular muscles," and has "found the sensibility

¹ H. Munk, "Ueber die Functionen der Grosshirnrinde, Gesammelte Mittheilungen," 4te Mittheilung, 1878.

of the conjunctiva and the reflex closure of the eyelids as distinct as in the normal condition."¹

Our experiments upon the occipital lobe have yielded no less definite *positive* results than those upon the angular gyrus yielded *negative*.

It may be mentioned in the first place, that we have had no difficulty in obtaining movements of the eyes by applying electrical stimulation to the occipital lobe, and I fail to understand how Dr. Ferrier was unable ever to succeed in getting the same result.² Even when no effect can be obtained from the angular gyrus, the surface of the occipital lobe gives a well-marked reaction even to weak excitations. Lueiani and Tamburini have also obtained positive results from excitation of the occipital lobe.

In illustration of the effects produced by complete removal of the occipital lobe, and of this alone, I will give two instances,

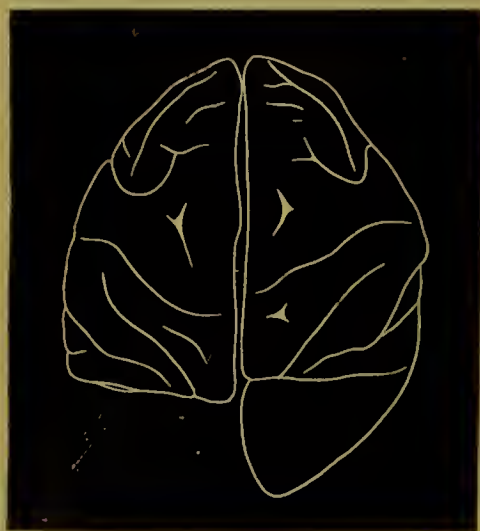


FIG. 2.—Brain of a Monkey, with complete removal of the left occipital lobe. Viewed from above.

in one of which the operation was unilateral, in the other bilateral.

In the monkey upon which the unilateral operation was performed, the left occipital lobe was removed by a vertical incision carried along the line of the parieto-occipital fissure.

¹ 'Functions of the Brain,' 2nd edition, p. 283.

² Ibid. pp. 244, 271, 288.

That the removal was exact and complete was confirmed on post-mortem examination, some eight months after the establishment of the lesion, when it was seen that the whole of the occipital lobe, and only this lobe, was involved (see Fig. 2), the angular gyrus being quite intact and normal, and the surface of the section looking as fresh, and showing as clearly the distinction of grey and white matter, as if the operation had but just been performed. The result was the immediate establishment of bilateral homonymous hemianopsia, which persisted during the whole time that the monkey was kept alive. Objects so placed that their images fell upon the left half of the retinae were taken no notice of: a threatened blow coming from the right-hand side of the mesial visual plane was not winced at or avoided; currants strewn upon the floor were only picked up towards the left side, the animal working round in that direction.

In the case of the monkey with a bilateral operation, the lesion was no less complete on both sides (Fig. 3). Here,

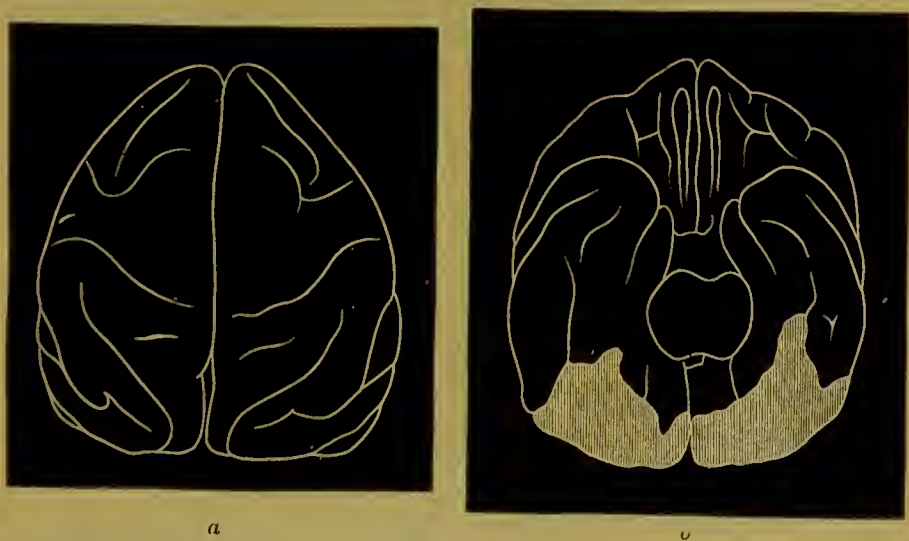


FIG. 3.—Brain of a Monkey, with complete removal of both occipital lobes. Viewed from above in *a*, and from below in *b*. On the under surface the lesion of the cortex, as shown by the shading, extends somewhat in advance of the limits of the occipital lobe.

again, the angular gyri were quite intact and perfectly healthy. The result was total and persistent blindness. The animal could only find food by groping and smelling. Brought into

a strange place, it ran against every obstacle. Placed in a dark room and with light flashed upon it, no signs of perception were given. Hearing was very acute, and all the other senses besides vision were unimpaired.

This monkey was in the same physiological condition as one described by Drs. Ferrier and Yeo,¹ and nearly all the description which they give of the behaviour of their animal is applicable to this one. In that case, however, they destroyed both angular gyri by the cautery, besides removing both occipital lobes bodily. It seems clear, however, from our experiment, that the destruction of the angular gyri was unnecessary, since precisely the same results are got when the occipital lobes alone are removed. This result was not, however, got by Drs. Ferrier and Yeo. When one or both occipital lobes were removed by them, they failed to obtain *any symptoms of defective visual perception*. This is, however, contrary to the statements of all other experimentalists, who have invariably obtained hemiopic symptoms transitory or permanent. The explanation may partly be that in Ferrier and Yeo's cases the removal was very incomplete. Thus, in experiment 9, they speak of having severed both occipital lobes with the galvanic cautery and scooped them out bodily. But on referring to the photographic representation of the brain, it is seen that only a small portion of each lobe has actually been removed. And it is the same with other experiments. This also applies, in some measure, to the experiments of Mr. Horsley and myself on the occipital lobes. On completely (as we thought) removing them, we obtained transient hemiopia or blindness, according as one or both sides were operated on. But the post-mortem examination showed that the removal, although more extensive than in Ferrier and Yeo's cases, was really in no instance complete.

Hitherto, Munk is the only observer who has stated that removal of the whole occipital lobe, and of this alone, in monkeys produces immediate and persistent hemiopia, or total blindness,² according as one or both sides are operated on. But there was always room to question the exact localisation

¹ *Op. cit.* experiment 12, p. 502.

² There seemed to be some doubt as to the persistence of total blindness.

of the lesion in Munk's experiments, because the operations were not antiseptic, and the neighbouring angular gyrus might have become subsequently involved. Moreover, Munk is chary of details, and gives no representations of the brains operated on, but merely a general diagram to illustrate his results.

It would appear, therefore, both from Munk's experiments and our own, that removal of the occipital lobe alone of one side is sufficient to produce permanent hemiopia, and that removal of this lobe on both sides of the brain is productive of complete blindness. But the following experiment shows (1) that, for the production of complete blindness, the removal of the lobe must be complete; and (2) that when a small portion of one of the lobes is left, although blindness is not complete, yet the limit of the visual field of the retinae may be greatly restricted. An operation was performed with the intention of removing entirely both occipital lobes, and it was done at about the same time, and on a monkey of the same kind and size as the animal whose case we have already related, and in which total blindness was produced. But in the present case the blindness was not quite absolute. From the first the animal appeared to distinguish between light and darkness, and to be conscious of the presence of large objects held between his eyes and the light. Soon (in a day or two) the visual perceptions became better marked, and it was found that, although objects whose images fell upon the upper part of the retinae remained entirely unnoticed—so that, for instance, food on the floor was not found, and blows aimed from below were not avoided—objects held above the horizontal visual plane were seen with greater or less distinctness, according to their position: those being most clearly seen and most unerringly seized which were held above (and perhaps a little to the right). It appeared, therefore, that this was a case indicating some localisation within the visual area. Munk has in fact described a correlation between the parts of the retina and of the occipital lobe as having been experimentally determined by him in dogs and monkeys.¹ It became, therefore, a matter of considerable interest to examine the brain, and to compare

¹ H. Munk, *op. cit.* 'Fünfte und siebente Mittheilungen.'

it with that of the other monkey with a similar lesion, but with total abolition of visual perceptions. It was found that in the latter case the lesion extended further forwards on the under surface of the brain than in the one in which vision was not totally abolished. The lesion was otherwise equally complete in both cases.

The exact superficial extent of the lesion is shown in Fig. 4.

No other lesions but these total removals of the occipital lobe have produced permanent blindness in our experiments ; but we have frequently got temporary hemiopia as a consequence of extensive lesions of the temporal lobe, and also

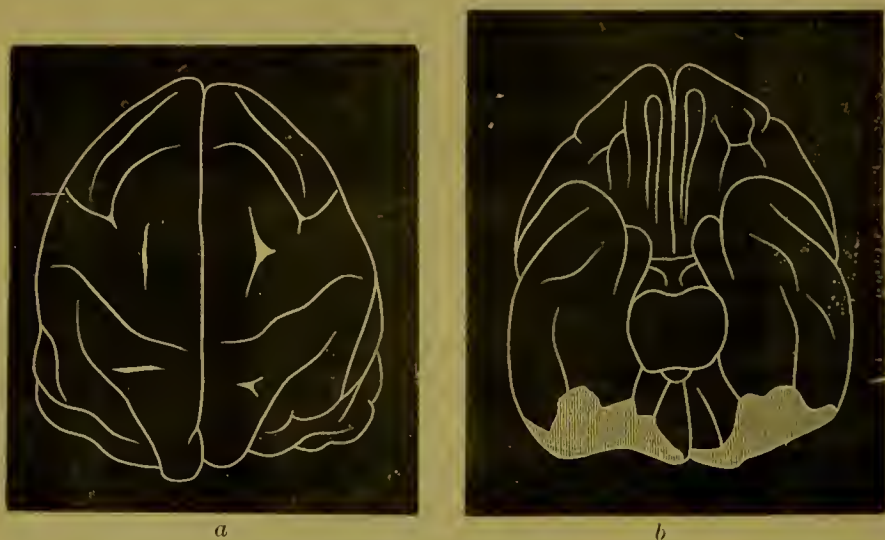


FIG. 4.—Brain of a Monkey, with complete removal of both occipital lobes. Viewed from above in *a*, and from below in *b*. It will be noticed that the cortical lesion does not extend so far forwards on the under surface in this brain as in the one shown in Fig. 3.

in one case (already related) of the angular gyrus. These transient symptoms may perhaps be ascribed rather to the disturbance in the circulation of the occipital lobe, and to the temporary loss of support which is afforded to that lobe by the adjoining parts of the brain, than to the fact, that the visual area of the cortex spreads over from the occipital lobe into the adjoining parts of the brain.¹ If this were the case in

¹ This is the view adopted by Luciani, "On Sensorial Localisation in the Cortex Cerebri;" 'BRAIN,' Vol. VII. 1884.

the monkey, there should be always some remains of the visual perceptive faculty after removal of the occipital lobes alone; whereas both Munk and ourselves have found that there may be no trace left of such faculty. The nearer to the occipital lobe that any such lesion of the temporal lobe is carried, the greater probability is there of the occurrence of (temporary) hemiopia, while extensive lesions of the more anterior parts of the brain fail to yield any sign of visual disturbance. It is, however, also possible that fibres connected with the cortex of the adjoining parts of the brain (and especially of the angular gyrus) may curve backwards into the occipital lobe, and thus become cut off along with that lobe. Various facts might be cited in support of this idea, and it would tend in great measure to reconcile the conflicting statements of experimentors on this region, but we are not yet in a position to come to a definite decision upon the subject.

I have further endeavoured, also in conjunction with Dr. Sanger Brown, to determine whether any evidence is to be obtained from monkeys regarding the localisation of the senses of hearing, smell, and taste. Respecting the sense of hearing, the opinion that has obtained most currency in this country is that of Dr. Ferrier, to the effect that it is entirely localised in the superior temporal gyrus; but, when we come to sift the experimental evidence in favour of this view, we find it to be very insufficient. It is briefly this, (1) that electrical excitation of this gyrus produces movements of the opposite ear (described as "pricking" by Ferrier) and of the head and eyes to the opposite side,¹ (2) that in one monkey destruction of this gyrus upon both sides of the brain has produced total and persistent deafness.² I call the evidence insufficient because, in the first place, excitation of very various parts of the cortex (frontal region, middle temporal gyrus, angular gyrus, and occipital lobe) produces almost precisely the same effects, and in the second place, because although it is not difficult to substantiate hearing in monkeys, it is difficult to substantiate deafness, for quite normal monkeys will often fail to pay the least attention even to loud sounds, and in a single

¹ Ferrier, 'Functions of the Brain,' 2nd edition, p. 305.

² Ferrier and Yeo, *op. cit.*, experiment 13.

ease which had been operated on such lack of attention might be erroneously ascribed to loss of hearing, unless it had been ascertained before the operation that the animal invariably reacted to certain noises.

We accordingly determined to repeat Dr. Ferrier's experiments in a number of monkeys. We had no difficulty in obtaining, as a result of electrical excitation of the superior temporal gyrus, the movement of the eyes towards the opposite side, the lids being usually at the same time raised. This effect occurs by excitation along about the posterior or superior two-thirds of the convolution, and it is not confined to this gyrus, but is also obtained on excitation of the adjoining part of the next temporal gyrus.¹ Excitation at the tip of the superior gyrus, just in the angle where the parallel and sylvian fissures meet, produces retraction of the opposite ear. We have not got the pricking forward of the ear which Dr. Ferrier describes.

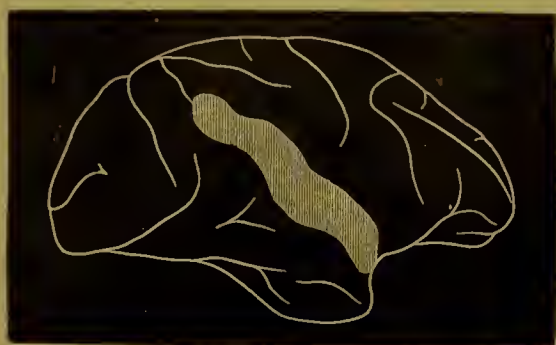
In six monkeys we have more or less completely destroyed the superior temporal gyrus upon both sides. I say more or less completely, because in one or two a small shred of grey matter belonging to this convolution was found post mortem, but practically the lesion was complete in all six, some of the grey matter within the fissures bounding the gyrus being all that could be taken to represent the convolution, and even this being deprived of its medullary centre. I have no hesitation in affirming that in every case the removal was as complete as—probably more complete than—in the monkey described by Ferrier and Yeo;² this I judge from the photographs of the brain and of the sections through it and from the woodcuts which Dr. Ferrier gives in his book,³ which are clearer than the photographs. But in order to make assurance doubly sure, we in one monkey, a large female *Rhesus*, separated up the fissures bounding the gyrus and scooped it out entirely from the very bottom of the fissures, so that not a trace of the convolution in question should remain (Fig. 5). In all six cases the result was the same.

¹ Compare Luciani and Tamburini, "Sulle Funzioni del Cervello; seconda comunicazione," 1879.

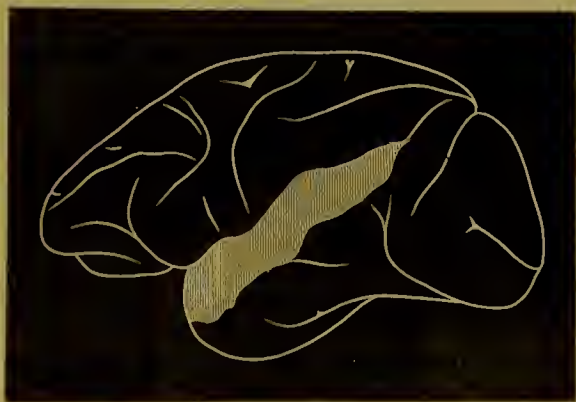
² Ferrier and Yeo, *op. cit.*, experiment 13.

³ 'Functions of the Brain,' 2nd edition, Figs. 97, 98.

learning was not only not permanently abolished, it was not perceptibly affected. The animals, even immediately after recovery from the anæsthetic, reacted to slight sounds of an unusual character, such as a smacking of the lips or the rustle of a crumpled newspaper. Some of them were under observation for several months, and there was never any doubt in our minds as to the full possession of their auditory faculties. Nor could the reactions they exhibited to sounds be explained by supposing that they only responded in a



a



b

FIG. 5.—Brain of a Monkey, with complete removal of both superior temporal gyri. The right side is shown in *a*, and the left side in *b*.

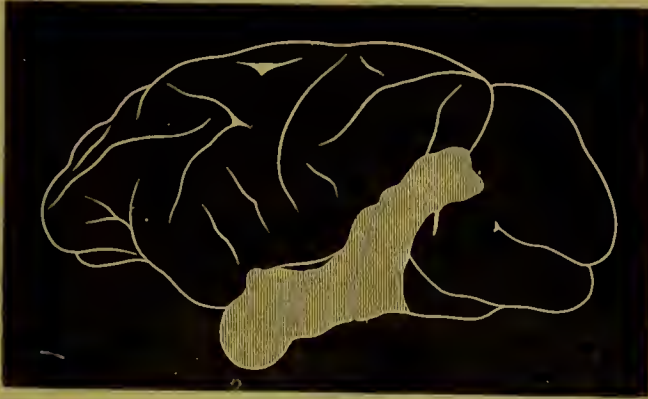
reflex manner, for they gave every evidence of understanding the nature of different sounds, such as that caused by turning a door-handle or the differences between the footsteps of different people; varying emotions being exhibited according to the anticipations (of food, &c.) which the sounds called forth.

One of the six monkeys had not only the superior temporal gyri removed, but the whole temporal lobe on both sides, the lesion extending as far as the hippocampal margin of the hemisphere (Fig. 6, *a, b, c*). This profound double lesion was effected in two operations, and at first produced a condition resembling idiocy, which was well marked for a few days, but afterwards gradually passed off. This condition was probably caused by the great disturbance of the functions of the whole brain which so extensive a removal produced, and especially the vascular disturbance caused by the occlusion of branches of the middle cerebral arteries. A similar condition was brought about in the large female *Rhæsus* above mentioned, in which both superior temporal gyri were radically removed after separating up the fissures bounding them, and here also there must have been considerable interference with the middle cerebral arteries.

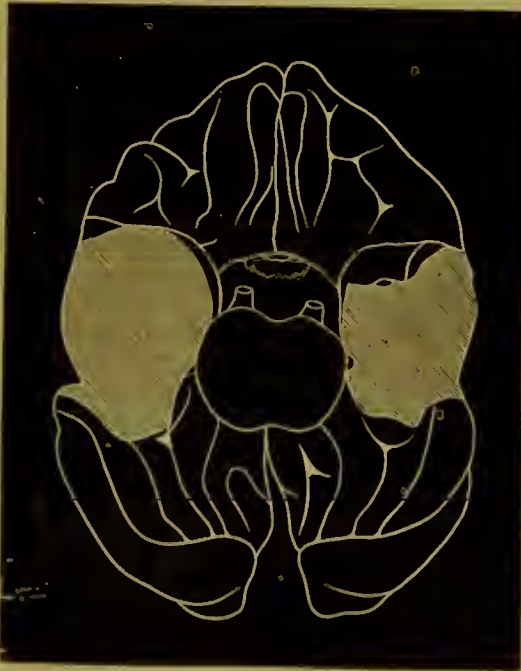
The condition was marked by loss of intelligence and memory, so that the animals, although they received and responded to impressions from all the senses, appeared to understand very imperfectly the meaning of such impressions. This was not confined to any one sense, and was most evident with visual impressions. For even objects most familiar to the animals were carefully examined, felt, smelt and tasted, exactly as a monkey will examine an entirely strange object, but much more slowly and deliberately. And on again, after only a few minutes, coming across the same object, exactly the same process of examination would be renewed, as if no recollection of it remained. The disposition also became completely changed: both animals exhibited the utmost greediness, losing all the daintiness which characterises the feeding of monkeys; they also entirely lost their fear of man. This idiotic condition lasted longer in the large female *Rhæsus* than in the monkey deprived of the whole of the temporal lobes, which in a few days had already almost entirely recovered memory and intelligence, while the former remained in a stupid condition for some weeks. But there was never any difficulty in observing that sounds, even slight in intensity, were heard. One of these animals was kept for eight, the other for nine months; and except for the condition just described, which



a



b



c

FIG. 6.—Brain of a Monkey, with almost complete removal of both temporal lobes. The brain is shown as seen from the right side in *a*, from the left side in *b*, and from below in *c*.

was only temporary, they behaved during the whole time in every way like normal monkeys.¹

The case of the monkey with both temporal lobes completely removed militates as strongly against the view, that the auditory perceptive faculty is *localised in those lobes*, as do the six cases against Dr. Ferrier's view. H. Munk appears to be of that opinion; but I cannot find any account of experiments which he has made upon *monkeys* in corroboration of the view; it appears to rest entirely upon experiments on dogs.² Luciani and Tamburini³ speak of the auditory centre in monkeys as being presumably situated in the superior and middle temporal gyri; but this opinion appears to be based merely on the results of electrical excitation. Luciani, in a later communication,⁴ remarks, "Our results tend to show that not only the whole cortical area of the temporal lobe, as admitted by Munk, but probably also the *cornu ammonis* forms an integral portion of the auditory sphere." With bilateral extirpation, "at first the auditory troubles may amount to absolute deafness, but soon pass into a condition of obtuseness of hearing. . . ."

Although it is not specially stated, it would appear that these statements (of Luciani) also rest mainly, if not entirely, on experiments on dogs. I believe, therefore, I am justified in asserting, that the supposed localisation of the auditory

¹ These two animals were exhibited to the Neurological Society, and a Committee of that Society was appointed to examine them. Another monkey which was erroneously believed to have been submitted to the same operation (removal of both superior temporal gyri), and a fourth, which had been subjected to no operation at all, were also put before the members of the Committee. No doubt was raised as to the hearing of the first two; but one member of the Committee thought that the third, and another member that the fourth, monkey was totally deaf! This I mention to illustrate the difficulty that even skilled observers, unacquainted with the habits and disposition of the individual animals, experience in deciding the question of the possession or loss of hearing in monkeys. We ourselves had obtained so many evidences from time to time by being frequently with the animals, that we never had the slightest doubt upon the subject; nor could any one that had much to do with them.

² *Op. cit.* 4te Mittheilung, Fig. 4, s. 63. In the description of this figure the author states, "Mit *B* ist die Rindenpartie bezeichnet, welche nach den Erfahrungen am Hunde als Hörsphäre anzunehmen ist." Munk regards the supero-posterior tip of the first temporal gyrus and the adjacent part of the angular gyrus as the "sensory area of the region of the external ear."

³ *Op. cit.*

⁴ "On Sensorial Localizations," etc., 'BRAIN,' Vol. VII. p. 154.

pereceptive faeulties in the temporal lobe in monkeys has no experimental evidence in its favour, and the ease I have described, in which both temporal lobes (including the *cornu ammonis*) were wholly removed without any permanent diminution in the acuteness of hearing, bears strongly against that view.

In the same animal smell and taste were also present, and, so far as we could ascertain, were in no way diminished in acuteness. This was also, as may *à fortiori* be expected, the case in two other monkeys, in which we cut away the antero-inferior extremity of the temporal lobe on both sides. These experiments were made previous to those of total extirpation of the lobe, and were intended to test Dr. Ferrier's surmise, that this region of the temporal lobe is related to the faeulty of taste.¹ But they give no support to that surmise (which is besides based on entirely insufficient evidence²), for all our animals gave well-marked evidences of taste both in the selection of favourite articles of food and in the disgust exhibited when a bitter substance, such as quinine, had been concealed within a raisin and thus inadvertently taken into the mouth.

With reference to the cerebral localisation of perceptions produced through the nerves of tactile and of general sensibility, I would recall the fact that, in the researches which I have before alluded to as having been carried on in conjunction with Mr. Horsley,³ we described a number of experiments upon monkeys in which a more or less extensive destruction of one gyrus fornicatus was produced; this lesion being invariably accompanied by a considerable diminution, or even by complete abolition, of tactile sensibility on the opposite side of the body, while at the same time there was also considerable loss of general sensibility. This condition was always followed

¹ 'Functions of the Brain,' 2nd edition, p. 321.

² Movements of the lips, tongue, and cheek-pouches on electrical excitation (which may well have spread to the superjacent motor area in the lower part of the frontal lobe) and certain earlier experiments in which lesions (not aseptic) were roughly produced in this part, and loss of taste seemed to follow. But the animals lived but a short time, and were in an entirely abnormal condition when tested, nor was the testing performed with purely sapid substances, but with acid and aromatic articles.

³ 'Philosophical Transactions,' 1888.

by partial recovery, which gradually supervened until a stationary condition of diminished sensibility appeared to be permanently established. We did not, however, keep any of our animals which had been subjected to this operation for more than about three months. In order, therefore, to determine if possible whether in such cases there was ultimate complete recovery, I removed in another monkey a portion of about one and a half centimetres in length (the whole brain being about six centimetres long) from the middle of the gyrus fornicatus, on the right side of the brain. This operation produced a condition of almost complete (hemi-) anæsthesia, involving the whole of the left side of the body with the exception of the forearm and hand. There was a little paresis of the leg, due apparently to a portion of the leg area in the superjacent marginal convolution having been accidentally injured in the operation, but none of the upper limb or of any other part of the body. As a rule, there was no reaction to touch, nor even to a slight prick applied to the anæsthetic side, and even when a movement followed, it was more like a reflex action than one dictated by the higher centres, for it was unaaccompanied by wincing, which was invariably produced when the other side of the body was suddenly touched or pricked.

This animal was kept under observation for more than seven months, and was tested from time to time. It was found that although the condition in question underwent some improvement, there was still during the whole of that time a marked difference in the two sides of the body, the left side, with the exception of the forearm and hand, which were never anæsthetic, being distinctly deficient in sensibility as compared with the right. We may fairly infer, therefore, that the hemianæsthesia which is produced by destructive injuries of the gyrus fornicatus is in all probability permanent. Whether however the perception of impressions of tactile and general sensibility is confined to the gyrus fornicatus and its continuation into the gyrus hippocampus, can only be effectually cleared up by the entire removal of these parts of the limbic lobe—an operation of the greatest difficulty, but one which I

have not given up hopes of ultimately effecting. In the meantime, I would affirm the extreme probability of this hypothesis on evidence obtained by exclusion, for I have never been able to determine the existence of any permanent diminution of sensibility after operations upon other parts of the cortex, unless there were a possibility of the limbic lobe having been directly or indirectly involved.

LONDON:
PRINTED BY WILLIAM CLOWES AND SONS, LIMITED,
STAMFORD STREET AND CHARING CROSS.